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STOMACH CONTENTS OF LONG-FINNED PILOT WHALES (*GLOBICEPHALA MELAS*) STRANDED ON THE U.S. MID-ATLANTIC COAST

DAMON P. GANNON
Department of Biology, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543, U.S.A.
Department of Biology, Bridgewater State College, Bridgewater, Massachusetts 02325, U.S.A.
Plymouth Marine Mammal Research Center, P. O. Box 1131, Plymouth, Massachusetts 02362, U.S.A.

ANDREW J. READ[1]
JAMES E. CRADDOCK
Department of Biology, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543, U.S.A.

JAMES G. MEAD
Division of Mammals, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560, U.S.A.

ABSTRACT

Ten prey taxa were recorded from the stomach contents of eight long-finned pilot whales (*Globicephala melas*) independently stranded along the U.S. mid-Atlantic coast. Relative importance of prey species was determined by methods that incorporate prey frequencies of occurrence, proportions of numerical abundance, and proportions of reconstructed mass. Separate analyses of trace (free, durable body parts representing well-digested prey items) and non-trace (relatively intact prey specimens) food material were conducted in order to address biases caused by differential rates of digestion and passage through the gastrointestinal tract. Different measures of prey importance yielded varying results, but the long-finned squid (*Loligo pealei*) was the most important prey species regardless of how prey importance was defined. Fishes were relatively unimportant in the diet. Our results indicate that the diets of western North Atlantic long-finned pilot whales differ substantially from what has been previously reported in the literature and that results from food-habits studies that utilize different techniques may not be comparable.

Key words: *Globicephala melas,* long-finned pilot whale, stomach contents, food habits, stranding, *Loligo pealei,* prey importance.

[1] Current address: Duke University Marine Lab, Beaufort, North Carolina 28516, U.S.A.

Whales of the genus *Globicephala,* including long-finned (*G. melas*) and short-finned (*G. macrorhynchus*) pilot whales, are thought to account for a large portion of the food energy consumed by cetaceans on the outer continental shelf of the northeastern United States north of Cape Hatteras (Kenney *et al.* 1985). *G. melas* has a more northern distribution than *G. macrorhynchus* (Winn 1982, Payne and Heinemann 1993) and is probably the most abundant of the two pilot whale species in this region (Payne and Heinemann 1993).

Our motivation for undertaking this project came from the realization that previous studies of *G. melas* food habits in the western North Atlantic have been characterized by low prey diversities relative to studies conducted in the eastern North Atlantic and the Southern Hemisphere (Table 1; hereafter, "pilot whale" refers to *G. melas*). We wanted to determine whether this difference was real or merely an artifact of differences in research methodologies used in the three areas. Two major pilot whale food-habits studies have been conducted in the western North Atlantic: Sergeant (1962) and Overholtz and Waring (1991). Using stomach contents data from animals taken in the Newfoundland drive fishery, Sergeant (1962) found that pilot whales primarily fed on the short-finned squid (*Illex illecebrosus*) and supplemented their diet with cod (*Gadus morhua*) when squid were scarce. Overholtz and Waring (1991) concluded from their study of five pilot whales incidentally captured by the pelagic mackerel fishery that Atlantic mackerel (*Scomber scombrus*) represented 71% of the diet and the remaining 29% consisted of long-finned squid (*Loligo pealei*) by existing mass.

In addition to these two food-habits studies in the western North Atlantic, three other papers contain brief information on stomach contents. Mercer (1967) reported that the stomachs of two pilot whales from an anomalous pod that overwintered in Newfoundland waters contained only Greenland turbot (*Reinhardtius hippoglossoides*). In a more recent report on the ecological relationship of pilot whales and *I. illecebrosus,* Mercer (1975) cited an observation of the squid *Gonatus fabricii* in the stomachs of 12 whales driven ashore in Newfoundland. In a paper on the incidental catch of marine mammals in foreign fisheries off the northeast United States, Waring *et al.* (1990) stated

Table 1. Number of prey species of long-finned pilot whales reported in the literature for three geographical regions (n = the number of stomachs examined).

	NW Atlantic[1] $n > 51$	NE Atlantic[2] $n > 861$	Tasmania[3] $n = 2$
Cephalopoda	3	15	14
Fishes	4	16	1
Crustacea	0	2	0
Others	0	4	0
TOTAL	7	37	15

From: Jensen 1916[2], Ritchie 1924[2], Sergeant 1962[1], Mercer 1967[1], Mercer 1975[1], Martin *et al.* 1987[2], Waring *et al.* 1990[1], Overholtz and Waring 1991[1], Gales and Pemberton 1992[3], Desportes and Mouritsen 1993[2].

that the stomachs of two pilot whales captured by the mackerel fishery contained only mackerel.

It should be noted that all of the studies in the western North Atlantic relied heavily on intact prey items to determine relative dietary importance, while work in other areas (*e.g.,* Martin *et al.* 1987, Gales and Pemberton 1992, Desportes and Mouritsen 1993) examined both intact and well-digested food material. Because of differences in digestion rates between fish and squid flesh (Bigg and Fawcett 1985), estimates of the dietary importance of cephalopods may be negatively biased when only intact prey are quantified or when existing prey mass is used.

Stomach contents of stranded animals may exhibit biases associated with the stranding event, but they do provide insight into dietary habits of the species. In this paper we describe the stomach contents of eight long-finned pilot whales that stranded independently along the mid-Atlantic coast of the United States. These eight stomachs represent the entire food-habits collection from stranded *G. melas* at the Smithsonian Institution's National Museum of Natural History. Several analytical methods were used to achieve a complete picture of the diet.

Methods

Sample collection—Stranding locations of the eight whales are plotted in Figure 1. Table 2 provides information on stranding location, date, gender, body length, and maturity status for each animal. Based on body length, individuals were classified as calves (not fully weaned), immature (nutritionally independent but sexually immature), or sexually mature.

Stomachs were removed, after the esophagus and intestine had been ligated, then transported to the Smithsonian Institution where they were temporarily stored frozen. Stomach contents were subsequently placed in 70% ethanol for long-term storage at the Smithsonian. During examination, all prey items were passed through a metal sieve with a mesh diameter of 1.0 mm to isolate hard parts.

Prey identification—Prey items were identified by comparing whole specimens, and parts thereof, to a laboratory reference collection, museum reference collections at the Smithsonian and the Harvard University Museum of Comparative Zoology, and published guides, including Flescher 1980, Clarke 1986*a,* Vecchione *et al.* 1989, and Roper *et al.* 1984. Structures used to identify partially digested food items included cephalopod lower beaks, teleost sagittal otoliths, teleost dentaries, skulls, squalid spines, and articulated vertebral columns.

Prey importance—Separate analyses of "trace" and "non-trace" (Bigg and Perez 1985) prey categories were conducted. Trace food items were those that were well digested and represented only by disarticulated skeletal elements, squid beaks, or squalid spines. The non-trace category consisted of relatively undigested food items. Whole specimens, fish heads with attached flesh, torsos, cephalopod mantles, buccal masses with beaks, and crowns (arms with buccal

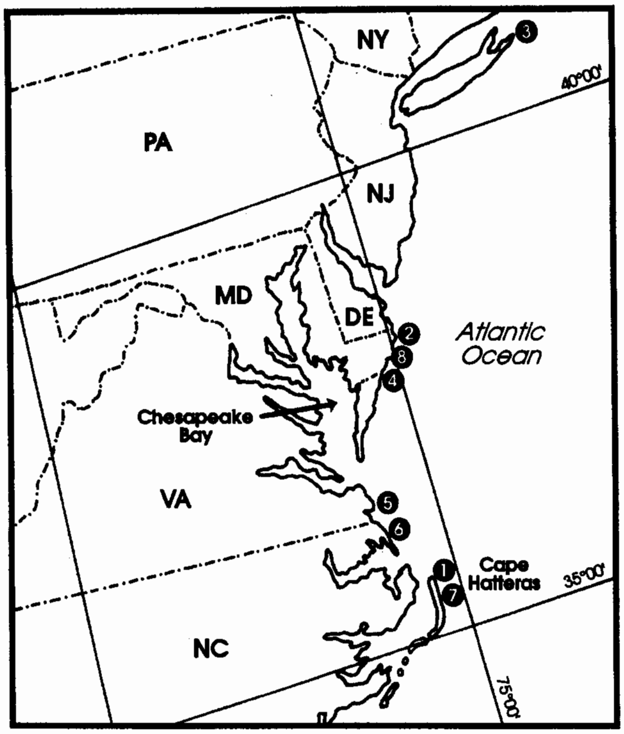

Figure 1. Stranding locations of long-finned pilot whales included in food-habits analyses.

Table 2. Summary of stranding data for long-finned pilot whales included in food-habits analyses (No. = identification number, Yr= Year, Mo = Month, D = Day, Len = Standard Length in Meters).

No.[1]	State	Yr	Mo	D	Len	Sex	Maturity[2]
1	NC	73	3	29	2.15	F	Calf
2	MD	77	5	05	3.04	M	Immature
3	NY	79	3	27	2.80	M	Calf
4	VA	82	4	12	3.95	M	Immature
5	VA	87	3	17	5.05	F	Mature
6	NC	87	4	21	3.88	F	Mature
7	NC	88	9	28	2.35	M	Calf
8	MD	93	4	10	4.05	F	Mature

[1] Correspond to numbers in Figure 1.
[2] From morphometric data given by Sergeant 1962, Kasuya *et al.* 1988, Bloch *et al.* 1993, Desportes *et al.* 1993, Martin and Rothery 1993.

Table 3. Regression equations used to estimate length (dorsal mantle length for squids, fork length for teleosts, and total length for squalids: L) and weight (W) of pilot whale prey items from otolith length (OL), dentary length (DL), and cephalopod lower rostral length (LRL). All lengths are in millimeters and weights are in grams.

Prey species	Regression equation	Source
Loligo pealei (long-finned squid)	$log\mathrm{L} = 1.767 + 1.4 log\mathrm{LRL}$ $\mathrm{W} = 0.25662(\mathrm{L}/10)^{2.15182}$	This study Lange and Johnson 1981
Ommastrephidae[1] (short-finned squid)	$ln\mathrm{W} = 1.773 + 2.40 ln\mathrm{LRL}$	Clarke 1962
Histioteuthidae[2]	$\mathrm{L} = -13.6 + 22.21\mathrm{LRL}$ $ln\mathrm{W} = 1.594 + 2.31 ln\mathrm{LRL}$	Clarke 1986*a* Clarke 1986*a*
Chiroteuthis veranyi	$ln\mathrm{W} = -0.241 + 2.7 ln\mathrm{LRL}$	Clarke 1980
Squalus acanthias (spiny dogfish)	$ln[(\mathrm{W} + 1)/1000] = 0.0293(\mathrm{L}/10) - 1.1714$ females ≥ 500 mm $ln[(\mathrm{W} + 1)/1000] = 0.0235(\mathrm{L}/10) - 0.8535$ males ≥ 500 mm	Nammack *et al.* 1985 Nammack *et al.* 1985
Scomber scombrus (Atlantic mackerel)	$\mathrm{L} = -10.04 + 12.66\mathrm{DL}$ $\mathrm{L} = 10(7.33\mathrm{OL} + 0.37)$ $\mathrm{W} = 0.00756(\mathrm{L}/10)^{3.082}$	This study Recchia and Read 1989 Kulka and Stobo 1981
Clupea harengus (Atlantic herring)	$\mathrm{L} = 69.23\mathrm{OL} - 27.48$ $log\mathrm{W} = 3.12 log\mathrm{L} - 5.41$	Recchia and Read 1989 Recchia and Read 1989
Merluccius bilinearis (silver hake)	$\mathrm{L} = 20.9\mathrm{OL} - 0.41$ $log\mathrm{W} = 3.08 log(\mathrm{L}/10) - 2.23$	Recchia and Read 1989 Kohler *et al.* 1970
Urophycis spp. (other hake)	$\mathrm{L} = (1.52\mathrm{OL}^{1.1456})10$ $\mathrm{W} = 0.003998(\mathrm{L}/10)^{3.1718}$	Bowen and Harrison 1994 Bowen and Harrison 1994

[1] Most of the ommastrephids were believed to be *Illex illecebrosus,* so the regression equation used to calculate ommastrephid mass was that given by Clarke (1962) for *I. illecebrosus.*

[2] Regressions are available for the family Histioteuthidae, but not for the species *Histioteuthis reversa.*

mass and beak) all qualified as non-trace. Analysis of trace prey was performed in order to address biases caused by differential rates of digestion.

Size of prey at ingestion was reconstructed by estimating mass from body length or the length of undigested hard parts (Clarke 1962, Kohler *et al.* 1970, Clarke 1980, Lange and Johnson 1981, Nammack *et al.* 1985, Clarke 1986*a,* Recchia and Read 1989, Bowen and Harrison 1994). Table 3 lists the regression equations used to estimate size of prey from otolith lengths, dentary lengths, cephalopod lower beak rostral lengths, and body lengths. The regression equation relating dorsal mantle length and lower rostral length for *Loligo pealei* was calculated using a sample of 25 specimens ($r^2 = 0.728$). Mackerel otoliths were very fragile, making them unsuitable for use in body-size estimation. Dentary bones were the most durable structures from mackerel, and we used these for identification and body-size estimation. Disarticulated dentaries were measured in a straight line from the anterior tip to the posterior margin, along the dorsal surface. The regression of fork length on dentary length for *Scomber scombrus* was estimated from a sample of 49 specimens ($r^2 = 0.993$). No length or weight regressions were available for *Selenoteuthis scintillans* (of the family Lycoteuthidae), a small squid growing to a mantle length of about 30 mm (Clarke 1986*a*). The three *S. scintillans* beaks recovered were assumed to represent an insignificant portion of the overall diet and were excluded from further analysis. Sexual dimorphism necessitated that separate length/weight regressions be calculated for male and female spiny dogfish, *Squalus acanthias* (Nammack *et al.* 1985). It was impossible to determine the sex of these ingested prey, so the reconstructed mass of each dogfish was the average of the mass of a male and a female of the corresponding length.

Left and right otoliths, left and right dentaries, and upper and lower beaks were separated, whenever possible. The minimum number of individuals present from each species was determined by the largest number of component parts from paired structures. When digestion precluded distinction of right and left otoliths, the total number of damaged otoliths from each species was divided by two in order to estimate the number of individual fish. All otoliths, dentaries, and beaks were counted, but only intact structures were measured to find the average size of each individual. Otoliths were categorized on a scale from 0 (undamaged otoliths retrieved from skulls) to 5 (severely degraded free otoliths) following the methods of Recchia and Read (1989). Otoliths categorized as 3 or higher were not used in size estimations, unless no undamaged otoliths were present. When intact hard parts were unavailable to estimate body size for a prey species in a particular stomach, the available skeletal structures were measured, which may have resulted in an underestimation of the mass represented by those structures. No mackerel dentaries recovered appeared to be damaged. Few squid beaks were too damaged to estimate size.

The relative importance of prey was measured by nine methods: (1) trace frequency of occurrence, (2) non-trace frequency of occurrence, (3) trace numerical abundance, (4) non-trace numerical abundance, (5) trace proportion of mass, (6) non-trace proportion of mass, (7) trace index of relative importance, (8) non-trace index of relative importance, and (9) "modified mass." Frequency of occurrence (FO) is the proportion of stomachs that contained a particular prey category, regardless of its mass or abundance. The denominator used in the calculation of trace frequency of occurrence is equal to the total number of stomachs in the sample that contained trace food remains ($n = 8$), while the denominator in non-trace FO is the number of stomachs that contained non-trace prey remains ($n = 4$). Proportion of numerical abundance (%Num) is the percentage of the total number of prey items recovered from all stomachs represented by a particular prey category. Proportion of reconstructed mass (%Mass) is the percentage of mass of prey at ingestion recovered from all stomachs represented by a particular prey category. Ingested prey mass was reconstructed to address biases caused by differential digestion rates. When diagnostic hard parts from more than 25 trace specimens of a prey taxon were present in one stomach, all hard parts from that taxon were tallied, and then a subsample of 25 was randomly selected and measured to estimate the average mass of individuals from that taxon in that particular stomach. Index of relative importance (IRI; Pinkas *et al.* 1971) combines the three methods already described and is calculated by the following equation:

$$\mathrm{IRI} = \mathrm{FO} \times (\%\mathrm{Num} + \%\mathrm{Mass})$$

The final method, modified mass, was adapted from the "modified volume" of Bigg and Perez (1985). It integrated frequency and mass measurements of both trace and non-trace food remains. Reconstructed mass was used rather than volume because we were interested in the sizes of prey at ingestion (and not the existing prey sizes after some unknown period of digestion, given the fact that different species digest at different rates). Prey items representing less than 1% of total mass were excluded from modified mass calculations (Bigg and Perez 1985). Modified mass was calculated by: (1) Determining the proportion of all fish to all squid by non-trace FO. (2) Determining the proportion of each species within these categories by total %Mass (trace and non-trace %Mass combined). (3) Adjusting the mass ratios for each species to sum to the total proportions of squid and fish present in the diet. (4). Readjusting all values to sum to 100%.

Some cephalopod beaks and teleost otoliths were not identified, either because they were not represented in reference collections or because they were severely damaged. All unidentified beaks were pooled and included in the calculations of trace frequency of occurrence and trace numerical abundance. Since the mass represented by these unidentified hard parts was unknown, they were excluded from reconstructed mass calculations.

Prey species compositions (measured by the above methods) were calculated for all eight whales as a group. Because of the small sample size, detailed investigations of potential dietary differences between age, sex, or reproductive categories were not possible.

Results

Table 4 lists the ten prey species identified in the stomachs of stranded pilot whales. The long-finned squid, *Loligo pealei,* was the most important prey item, regardless of how prey importance was defined (Tables 5 through 7). Measures of prey importance for *L. pealei* ranged from 47.4% (modified mass) to 93.8% (non-trace numerical abundance) of the overall diet. Pilot whales fed on *L. pealei* ranging in size from 50 to 420 mm mantle length, but most were between 100 and 300 mm (Fig. 2). The largest *L. pealei* weighed approximately 798 g. *Histioteuthis reversa* and squids of the family Ommastrephidae consistently ranked in the top three prey taxa by trace measures (Table 5). Ommastrephids and *H. reversa* were present in 62.5% and 50% of stomachs, respectively, but were not represented by any non-trace specimens. Un-

Table 4. List of prey species present in the stomachs of long-finned pilot whales stranded along the U.S. mid-Atlantic coast, with their associated trace and non-trace abundances.

Species name	Common name	No. of trace specimens	No. of non-trace specimens
FISHES			
Clupea harengus	Atlantic herring	8	0
Merluccius bilinearis	Silver hake	4	0
Scomber scombrus	Atlantic mackerel	2	2
Squalus acanthias	Spiny dogfish	3	3
Urophycis spp.	Hake (red, white)	5	0
Unknown fish		1	0
SQUIDS			
Chiroteuthis veranyi		87	0
Histioteuthis reversa		221	0
Loligo pealei	Long-finned squid	560	75
Ommastrephidae	Short-finned squid	184	0
Selenoteuthis scintillans		3	0
Unknown squid		62	0

identified squid beaks were present in four stomachs and represented 5.1% of the trace numerical abundance.

Fish were relatively unimportant in the diet of these eight animals. Surprisingly, spiny dogfish, present only in one stomach, appeared to be the most important fish species. The contribution of dogfish to the overall diet ranged from 0.3% (trace numerical abundance) to 38.3% (non-trace proportion of

Table 5. Frequency of occurrence (FO), proportion of numerical abundance (%Num), and proportion of reconstructed mass (%Mass), with associated ranks (#), for the trace food materials of long-finned pilot whales stranded along the U.S. mid-Atlantic coast.

Species	Trace FO		Trace %Num		Trace %Mass	
	%	#	%	#	%	#
L. pealei	75.0%	1	49.1%	1	73.1%	1
Ommastrephidae	62.5%	2	16.1%	3	12.4%	2
H. reversa	50.0%	3	19.4%	2	7.1%	3
S. acanthias	12.5%	7	<1%	6	4.3%	4
C. veranyi	50.0%	3	7.6%	4	1.5%	5
C. harengus	12.5%	7	<1%	6	1.3%	6
S. scombrus	12.5%	7	<1%	6	<1%	7
Urophycis spp.	12.5%	7	<1%	6	<1%	7
M. bilinearis	12.5%	7	<1%	6	<1%	7
S. scintillans	37.5%	6	<1%	6	—	—
Unknown squid	50.0%	3	5.1%	5	—	—
Unknown fish	12.5%	7	<1%	6	—	—

Table 6. Frequency of occurrence (FO), proportion of numerical abundance (%Num), and proportion of reconstructed mass (%Mass), with associated ranks (#), for the non-trace food materials of long-finned pilot whales stranded along the U.S. mid-Atlantic coast.

	Non-trace FO		Non-trace %Num		Non-trace %Mass	
Species	%	#	%	#	%	#
L. pealei	75.0%	1	93.8%	1	51.9%	1
S. acanthias	25.0%	2	3.8%	2	38.3%	2
S. scombrus	25.0%	2	2.5%	3	9.8%	3

mass). Dogfish rivaled long-finned squid in non-trace mass (Table 6) and modified mass (Table 7), even though only six individuals were recovered (three intact and three trace). Each dogfish was about 750 mm in length and weighed about 1,640 g. Atlantic mackerel contributed a minimum of 0.2% to the overall diet when measured by either trace numerical abundance or trace proportion of mass, and a maximum of 25% when measured by non-trace frequency of occurrence. Unidentified otoliths were present in one stomach and represented 0.08% of the diet by trace numerical abundance. Dietary importance rankings of the three species represented by non-trace specimens were all in agreement, with long-finned squid first, spiny dogfish second, and Atlantic mackerel third (Table 6). *Chiroteuthis veranyi, Selenoteuthis scintillans, Clupea harengus,* and *Merluccius bilinearis* were found only as trace items and comprised a small part of the diet (Table 5).

Discussion

The most striking aspect of these data was the strong dominance of *Loligo pealei* in every prey importance category. The relatively high prey diversity was also noteworthy. Of the ten prey species identified, *Clupea harengus, Mer-*

Table 7. Trace and non-trace indices of relative importance (IRI) and modified mass, with associated ranks (#), for the prey of long-finned pilot whales stranded along the U.S. mid-Atlantic coast.

	Trace		Non-trace			
Species	IRI	#	IRI	#	Mod. mass	#
L. pealei	0.92	1	1.09	1	47.4%	1
S. acanthias	0.01	5	0.11	2	30.6%	2
Ommastrephidae	0.18	2	—	—	7.4%	3
C. harengus	<0.01	6	—	—	4.7%	4
S. scombrus	<0.01	6	0.03	3	4.6%	5
H. reversa	0.13	3	—	—	4.3%	6
C. veranyi	0.05	4	—	—	<1%	7
Urophycis spp.	<0.01	6	—	—	—	—
M. bilinearis	<0.01	6	—	—	—	—

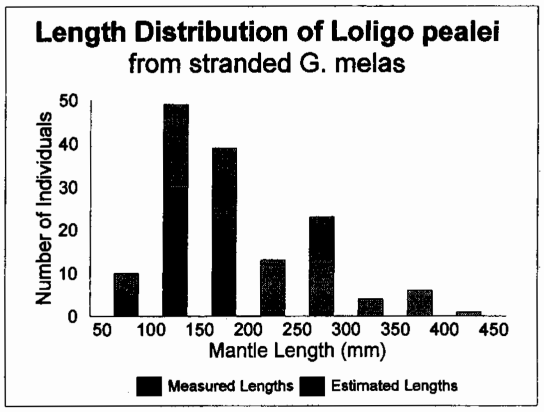

Figure 2. Length frequency distribution of *Loligo pealei* recovered from the stomach contents of stranded long-finned pilot whales.

luccius bilinearis, Squalus acanthias, Urophycis spp., *Chiroteuthis veranyi,* and *Selenoteuthis scintillans* have never before been reported in the diet of long-finned pilot whales. *Histioteuthis reversa* had previously only been known from pilot whales in the eastern North Atlantic (Desportes and Mouritsen 1993). Ten prey species were represented by trace specimens, while only three prey species had non-trace representatives. Previous studies in the Northwest Atlantic only analyzed intact, or non-trace, food material (Sergeant 1962, Mercer 1967, Mercer 1975, Waring *et al.* 1990, and Overholtz and Waring 1991), while studies in other regions utilized trace and non-trace remains (Martin *et al.* 1987, Gales and Pemberton 1992, Desportes and Mouritsen 1993). Our results indicate that the diet of western North Atlantic long-finned pilot whales differs substantially from that described previously, both in terms of diversity and relative species importance. Furthermore, the apparent difference in prey diversities noted between studies in the Northwest Atlantic and those in other regions seems to have been caused by differences in the treatment of trace and non-trace food remains.

Estimated dietary contributions of each prey species varied widely among the nine methods used to assess relative prey importance, indicating that it is difficult to make comparisons among food-habits studies that utilize different methodologies. Each method measures different parameters and each contains biases. For example, squid flesh has been shown to digest faster than fish flesh in the stomachs of marine mammals (Bigg and Fawcett 1985). Squid beaks, however, are resistant to breakdown by gastric activity and are known to persist in the stomachs of predators, while fish, including soft tissue and bones, are digestible (Bigg and Fawcett 1985). Therefore, analyses which take only intact items into account are likely to underestimate the importance of cephalopods. Studies which examine all stomach contents in one data set are liable to overestimate the importance of cephalopods. This is demonstrated in our data by the paucity of squid species represented by non-trace specimens. Since the relative magnitudes of these biases are unknown, it is best to use a variety of trace and non-trace techniques in order to gain a more complete understanding of the diet.

Frequency-of-occurrence methods can overstate the importance of small or infrequently consumed prey, since neither prey size nor abundance is considered (Hyslop 1980, Bigg and Fawcett 1985, Bigg and Perez 1985, Pierce and Boyle 1991). Likewise, numerical abundance methods also exaggerate the contribution of small species. The concept behind IRI is that biases associated with the three component methods (FO, %Num, and %Mass) will be cancelled out by each other. However, because some biases afflict more than one component method, errors are probably compounded (Hyslop 1980). Of the methods used here, modified mass is perhaps the best single measure of relative prey importance, since it integrates non-trace frequency of occurrence, trace reconstructed mass, and non-trace reconstructed mass in a way that minimizes the effect of accumulated non-digestible parts (*i.e.,* squid beaks).

Because the lactation period is highly variable (Martin and Rothery 1993), body length is not a reliable indicator of nutritional independence for young pilot whales. However, we believed that it was important to have some knowledge about the extent to which our results may have been influenced by the inclusion of calves, which probably had a mixed diet of milk and solid food, and length was the only available criterion by which to make this judgment. We noted several gross differences between the stomach contents of the three calves and those of the older animals. The solid portion of the calf diet was generally characterized by: (1) small squids; (2) an absence of *Loligo pealei* (calf stomachs contained an average of 0.3 *L. pealei* beaks, while the entire sample averaged 79.4 *L. pealei* beaks per stomach); (3) few prey items (calf stomachs contained an average of 10 prey items compared to an average of 153 for the entire sample); (4) an absence of non-trace food remains; and (5) a complete lack of fish remains. Thus, it is likely that there are age-related dietary differences and that our results represent the combined diets of weaning calves and older, nutritionally independent animals. The prolonged weaning period is a learning stage during which calves probably experiment with solid food that is easy to capture. Smith and Read (1992) documented a transitional diet in weaning harbor porpoise (*Phocoena phocoena*) calves. Porpoise calves supplement milk obtained from their mothers with small, slow-moving euphausiids. By the time they are fully weaned, the diet of porpoise calves resembles that of adults and primarily consists of finfish (Read *et al.* 1994).

The limitations of food-habits data obtained from stranded marine mammals must be taken into account when interpreting these results. Our sample may have been biased toward nearshore prey (Clarke 1986*b*) or food that is not usually an important part of the diet. Illness, either caused by or resulting in malnutrition, can precipitate stranding. Nonetheless, the dietary composition of this sample is similar to that obtained from 30 pilot whales captured in the continental slope waters by the pelagic mackerel fishery (Gannon 1995). Based on a comparison of cetaceans collected at sea and from strandings, Ross

(1979) concluded that his sample of stranded animals provided representative dietary information.

Investigations that utilize small sample sizes, such as this, are vulnerable to biases. A skewed representation of the diet might be obtained if any animal had recently consumed prey that is not regularly eaten. This may account for the unexpectedly high level of importance given to the spiny dogfish. The large size difference between the dogfish and all other prey hints that dogfish might not be eaten frequently. The present sample included a very narrow segment of the population, collected predominantly during the spring. No adult males and no immature females were present. Therefore, potential dietary differences associated with sex, maturity status, and season could not be investigated. In the future, we hope to examine a larger sample with representatives from each age/sex class and each season, including animals obtained from mass strandings and incidental fishery captures.

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Literature Cited

Bigg, M. A., and I. Fawcett. 1985. Two biases in diet determination of northern fur seals (*Callorhinus ursinus*). Pages 284–291 *in* J. R. Beddington, R. J. H. Beverton and D. M. Lavigne, eds. Marine mammals and fisheries. George Allen & Unwin Ltd., London, UK.

Bigg, M. A., and M. A. Perez. 1985. Modified volume: A frequency-volume method to assess marine mammal food habits. Pages 277–283 *in* J. R. Beddington, R. J. H. Beverton and D. M. Lavigne, eds. Marine mammals and fisheries. George Allen & Unwin Ltd., London, UK.

Bloch, D., C. Lockyer and M. Zachariassen. 1993. Age and growth parameters of long-finned pilot whales off the Faroe Islands. Report of the International Whaling Commission (Special Issue 14):163–208.

Bowen, W. D., and G. D. Harrison. 1994. Offshore diet of grey seals, *Halichoerus grypus,* near Sable Island, Canada. Marine Ecology Progress Series 112:1–11.

Clarke, M. R. 1962. The identification of cephalopod beaks and the relationship between beak size and total body weight. Bulletin of the British Museum of Natural History 8:419–480.

Clarke, M. R. 1980. Cephalopoda in the diet of sperm whales of the southern hemisphere and their bearing on sperm whale biology. Discovery Reports 37:1–324.

CLARKE, M. R., ed. 1986*a*. A handbook for the identification of cephalopod beaks. Oxford University Press, Oxford, UK.

CLARKE, M. R. 1986*b*. Cephalopods in the diet of odontocetes. Pages 281–322 *in* M. M. Bryden and R. Harrison, eds. Research on dolphins. Clarendon Press, Oxford, UK.

DESPORTES, G., AND R. MOURITSEN. 1993. Preliminary results on the diet of long-finned pilot whales off the Faroe Islands. Report of the International Whaling Commission (Special Issue 14):305–324.

DESPORTES, G., M. SABOUREAU AND A. LACROIX. 1993. Reproductive maturity and seasonality of male long-finned pilot whales, off the Faroe Islands. Report of the International Whaling Commission (Special Issue 14):233-262.

FLESCHER, D. D. 1980. Guide to some trawl-caught marine fishes from Maine to Cape Hatteras, North Carolina. NOAA Technical Report, NMFS Circular 431. 35 pp.

GALES, R., AND D. PEMBERTON. 1992. Stomach contents of long-finned pilot whales (*Globicephala melas*) and bottlenose dolphins (*Tursiops truncatus*) in Tasmania. Marine Mammal Science 8:405–413.

GANNON, D. P. 1995. Foraging ecology of Northwest Atlantic long-finned pilot whales, *Globicephala melas* (Traill 1809). M.A. thesis, Bridgewater State College, Bridgewater, MA 02325. xv + 115 pp.

HYSLOP, E. J. 1980. Stomach contents analysis—a review of methods and their application. Journal of Fish Biology 17:411–429.

JENSEN, A. S. 1916. On some misinterpreted markings in the skin of the caa'ing whale. Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i Kjobenhavn 67:1–8.

KASUYA, T., D. E. SERGEANT AND K. TANAKA. 1988. Re-examination of life history parameters of long-finned pilot whales in the Newfoundland waters. Scientific Reports of the Whales Research Institute, Tokyo 39:103–119.

KENNEY, R. D., M. A. M. HYMAN AND H. E. WINN. 1985. Calculation of standing stocks and energetic requirements of the cetaceans of the Northeast United States outer continental shelf. NOAA Technical Memorandum, NMFS-F/NEC-41. 99 pp.

KOHLER, A. C., D. N. FITZGERALD, R. G. HALLIDAY, J. S. SCOTT AND A. V. TYLER. 1970. Length-weight relationships of the Canadian Atlantic region. Fisheries Research Board of Canada Technical Report No. 164. 12 pp. + 199 tables.

KULKA, D. W., AND W. T. STOBO. 1981. Winter distribution and feeding of mackerel on the Scotian shelf and outer Georges Bank with reference to the winter distribution of other finfish species. Canadian Technical Report of Fisheries and Aquatic Sciences 1038. 38 pp.

LANGE, A. M., AND K. L. JOHNSON. 1981. Dorsal mantle length-total weight relationships of squids *Loligo pealei* and *Illex illecebrosus* from the Atlantic coast of the United States. NOAA Technical Report, NMFS SSRF-745. 18 pp.

MARTIN, A. R., AND P. ROTHERY. 1993. Reproductive parameters of female long-finned pilot whales (*Globicephala melas*) around the Faroe Islands. Report of the International Whaling Commission (Special Report 14):263–304.

MARTIN, A. R., P. REYNOLDS AND M. G. RICHARDSON. 1987. Aspects of the biology of pilot whales (*Globicephala melaena*) in recent mass strandings on the British coast. Journal of Zoology (London) 211:11–23.

MERCER, M. C. 1967. Wintering of pilot whales, *Globicephala melaena,* in Newfoundland inshore waters. Journal of the Fisheries Research Board of Canada 24:2481–2484.

MERCER, M. C. 1975. Modified Leslie-Delury population models of the long-finned pilot whale (*Globicephala melaena*) and annual production of the short-finned squid (*Illex illecebrosus*) based upon their interaction at Newfoundland. Journal of the Fisheries Research Board of Canada 32:1145–1154.

NAMMACK, M. F., J. A. MUSICK AND J. A. COLVOCORESSES. 1985. Life history of spiny dogfish off the northeastern United States. Transactions of the American Fisheries Society 114:367–376.

Overholtz, W. J., and G. T. Waring. 1991. Diet composition of pilot whales *Globicephala* sp. and common dolphins *Delphinus delphis* in the Mid-Atlantic Bight during Spring 1989. Fishery Bulletin, U.S. 89:723–728.

Payne, P. M., and D. W. Heinemann. 1993. The distribution of pilot whales (*Globicephala* spp.) in shelf/shelf-edge and slope waters of the northeastern United States, 1978–1988. Report of the International Whaling Commission (Special Report 14):51–68.

Pierce, G. J., and P. R. Boyle. 1991. A review of methods for diet analysis in piscivorous marine mammals. Oceanography and Marine Biology 29:409–486.

Pinkas, L., M. S. Oliphant and I. L. K. Iverson. 1971. Food habits of albacore, bluefin tuna, and bonito in California waters. California Department of Fish and Game, Fish Bulletin 152:1–105.

Read, A. J., J. E. Craddock and D. Gannon. 1994. Life history of harbour porpoises and pilot whales taken in commercial fishing operations off the northeastern United States. Final Report (Phase II), Contract no. 50-EANE-2-00082, 91 pp. U.S. Department of Commerce, NOAA/National Marine Fisheries Service, Northeast Fisheries Science Center, Woods Hole, MA, 02543.

Recchia, C. A., and A. J. Read. 1989. Stomach contents of harbour porpoises, *Phocoena phocoena* (L.), from the Bay of Fundy. Canadian Journal of Zoology 67:2140–2146.

Ritchie, J. 1924. Observations on a pilot whale stranded in the Firth of Forth. Scottish Naturalist for 1924:37–43.

Roper, C. F. E., M. J. Sweeney and C. E. Nauen. 1984. FAO species catalogue. Cephalopods of the world. An annotated and illustrated catalogue of species of interest to fisheries. FAO Fisheries Synopsis Vol. 3. 277 pp.

Ross, G. J. B. 1979. The smaller cetaceans of the south east coast of southern Africa. Ph.D. thesis, University of Port Elizabeth. 415 pp.

Sergeant, D. E. 1962. The biology of the pilot or pothead whale *Globicephala melaena* in Newfoundland waters. Bulletin of the Fisheries Research Board of Canada 132. 84 pp.

Smith, R. J., and A. J. Read. 1992. Consumption of euphausiids by harbour porpoise (*Phocoena phocoena*) calves in the Bay of Fundy. Canadian Journal of Zoology 70: 1629–1632.

Vecchione, M., C. F. E. Roper and M. J. Sweeney. 1989. Marine flora and fauna of the eastern United States: Mollusca: Cephalopoda. NOAA Technical Report, NMFS 73. 23 pp.

Waring, G. T., P. Gerrior, P. M. Payne, B. L. Parry and J. R. Nicolas. 1990. Incidental take of marine mammals in foreign fishery activities off the Northeast United States, 1977–88. Fishery Bulletin, U.S. 88:347–360.

Winn, H. E., ed. 1982. A characterization of marine mammals and turtles in the mid- and North Atlantic areas of the U.S. outer continental shelf, Final Report. Final Report of the Cetacean and Turtle Assessment Program by the University of Rhode Island, Graduate School of Oceanography to the U.S. Department of the Interior, Bureau of Land Management. NTIS Publication PB83-215855. 586 pp.

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